

THE INHERITANCE OF LENGTHS OF WINGS AND PRONOTA
IN THE GROUSE LOCUST TETTIGIDEA PARVIPENNIS
MORSE AND T. P. PENNATA MORSE

by

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INTRODUCTION

Dimorphism with respect to wing length is common among several genera of the Acridian sub-family Tetriginae (grouse locusts). The most conspicuous characteristic of this sub-family is the large pronotum, which partakes also of the dimorphic character of the wings, macropterous forms having pronota almost as long as the wings, and brachypterous forms showing abbreviated pronota approximately the same length as the wings.

In these, and in other Orthoptera, some individuals are long winged; while others, unquestionably of the same species, are short winged. Whether the causal forces underlying this phenomenon of wing variation within a species are environmental or hereditary has been a subject for much discussion. This study is concerned with the question as it relates to Tettigidea parvipennis pennata Morse, and T. parvipennis Morse, two of the forms of grouse locusts being bred in the greenhouse laboratory of the K.S.C. Agricultural Experiment Station. It is known that characters such as color pattern variegations in these forms, and in the genera Apotettix, Paratettix, and others, are governed by hereditary units. An attempt has therefore been made to ascertain

whether wing length in Tettigidea may also be due to an heritable factor, or factors, or whether it must be attributed to environmental influences.

REVIEW OF LITERATURE

As far as can be ascertained, no formal experimentation has hitherto been reported regarding wing lengths of the species of Tettigidea. From several years' observations, however, of the incidence of long and short wingedness among these forms reared in the greenhouse, Nabours and MacQueen (1937) have come to regard the variation as hereditary, brachypterism being due to a dominant Mendelian gene, and macropterism to its recessive allelomorph.

Theories advanced by others have been based upon field observations or examination of museum collections. Morse (1904) has proposed that in Orthoptera showing wing dimorphism, the apterous or brachypterous forms, being flightless, predominate on alpine summits and on islands, due to natural selection through the agency of the wind, which carries the long winged ones away.

Morse (1904, 1905) considered the abbreviated condition a special structural adaptation to sylvan habitats. This contention was supported by Rehn and Hebard (1916) whose

data were collected in Indiana, and by Ball (1897) in Iowa. Morse likewise recognized geographical variations, the brachypterous forms being three times as plentiful in New England as the macropterous; while in Arkansas the condition was reversed. Blatchley (1920) found all specimens collected in Florida to be long winged, while in Indiana a small proportion of the short winged form were interspersed. In the vicinity of Chicago, the two types were found in approximately equal numbers (Nabours, 1914).

The wing and pronotum dimorphism in Tettigidea is thus a widely distributed characteristic, apparently varying both with immediate habitat and with general geographic location. Although the literature cited seems to favor the potency of environment in determining structure, experimental verification for such theories is lacking.

Valuable as bases for comparison are the data concerning dimorphism in other Tetrigian genera reared in the greenhouse; e.g., Apotettix eurycephalus Hancock and Paratettix texanus Hancock (Nabours 1914, 1925, 1937; Dean, 1933). These forms, collected from habitats in southern Texas, Louisiana, and in eastern Mexico, show two rather distinct wing phases. Regardless of parental types, pronotum and wing lengths "appear to be conditioned by the environment, or the time of year during which growth pro-

ceeds. In the spring when growth is rapid and the period short, the wings and pronota are preponderantly long. In the late summer, autumn, and early winter when growth is slow and the period long, short wings and pronota prevail". (Nabours, 1925).

In Apotettix eurycephalus, a parthenogenetic line was maintained for eleven generations (Dean, 1933), giving 107 offspring, both long and short winged. It was shown that, of the 67 individuals which grew to maturity during spring and summer months, 87.2 per cent were long winged and 12.8 per cent short winged. Among the 40 others, which matured in fall and winter, there were only 18.34 per cent long winged, and 81.66 per cent short winged. It thus appeared, since the genetic composition of these specimens was identical, that the seasonal effects upon their development were well established.

It should be noted, however, that siblings from the same egg clump may show striking differences in the speed with which they reach maturity (Nabours, 1914). From a brood hatched in late summer, some individuals may pass rapidly through nymphal ecdyses and become long winged adults before the season of retarded growth sets in. Others of the brood, apparently exposed to similar surroundings, may spend most of the winter reaching short winged maturity.

The question arises, therefore, as to the possibility of an hereditary complex which may cause siblings to give different reactions to the same environment. Attempts to discover such a factor or factors have so far resulted negatively.

Studies of other dimorphic or polymorphic Orthoptera include work on the Gryllidae (Lutz, 1908). Environmental conditions during the growth period of the crickets are credited as the determining factors in development. Faure (1932) has drawn similar conclusions from work with Locustana pardalina Walker, which is dichromatic as well as dimorphic. Morse (1904) notes other Orthoptera in which habitat and wing morphology show close correlation; viz., Microcentrum, Cyrtophyllus, and Oecanthus, which are brachypterous, and arboreal in habitat; Myrmecophila, Cryptocercus, and numerous Blattidae, which are also short winged and live in crevices and burrows. In contrast to these is Conocephalus, which lives on open, grassy land, and is prevailingly macropterous.

MATERIAL AND METHODS

Classification and Description

Of the eighteen North American species referred by Hancock (1902) to the genus Tettigidea, seven are distinct species native to Central America and Mexico (Morse, 1900, 1901). Eight others, covering a range from southeastern Canada to Honduras, are generally recognized as separate species. The three groups remaining, in which are included the subjects of this experiment, present such lack of uniformity in nomenclature as to make accurate classification difficult.

These three, accorded species rank by Hancock, are T. lateralis Scudder, T. parvipennis pennata Morse, and T. medialis Hancock. There are, in addition, the two brachypterous varieties of T. lateralis and T. p. pennata: T. polymorpha Scudder, and T. parvipennis Morse.

Blatchley (1901) and Kirby (1910) classify these forms as geographical races of one species described by Say (1824), T. lateralis. Kirby lists also the following synonyms: Tetrix parvipennis Harris and Tetrix polymorpha Burmeister, both short winged varieties; Tetrix lateralis parvipennis Harris, and Tettix lateralis Glover.

Whether they comprise true species or merely races, the specimens under observation in the greenhouse fall into three morphological groups. They all bear the distinguishing marks of the genus: relatively large bodies, sturdy legs; markedly compressed frontal costa advanced before the eyes; rather short antennae consisting of 22 articles; granulose body surface with more or less pronounced vein-like longitudinal rugulae on the dorsum of the pronotum; sexual dimorphism marked, females being more robust and on an average 3 mm. longer than males; arcuate-elevated median pronotal carina in all nymphal stages, producing a distinctly arched dorsal profile; color variegations limited to comparatively dull earth-hues; ferruginous, fuscous, or light clay-tones.

Bellamy (1917) has classified these locusts as T. parvipennis pennata Morse. His specimens were brought from the vicinity of Houston, Texas, by Nabours in 1914.⁽¹⁾ Of the three types distinguishable in the present stock, one appears to resemble closely the specimens used by Bellamy. These are robust, long winged specimens, which may be recognized as T. p. pennata by the obtuse-angulate anterior

(1) In permanent record books of the Zoology Laboratory.

margin of the pronotum, which projects over the occiput; by the white front of the male; and by the color patterns.

They are progeny of individuals brought from southern Texas and Mexico in 1929, 1933, 1934, 1936, and 1937.⁽¹⁾

The second type constitutes about one-half the total greenhouse stock of Tettigidea. These are brachypterous specimens collected chiefly in the vicinity of Manhattan, Kansas, which conform closely to Hancock's description of T. parvipennis, the short winged variety of those described above. In appearance these are distinguishable from T. p. pennata only by their abbreviated pronota and wings. The average amount of differentiation between the two varieties is shown by measurements of 300 preserved specimens of each type. Positive numbers indicate the distance which wings and pronota are extended beyond, and negative numbers the amount by which they fall short of, the distal ends of the posterior femora. No truly intermediate individuals were observed:

Macropterous

males	- pronotum	.976 mm.
	wings	2.88 mm.
females	- pronotum	.991 mm.
	wings	2.75 mm.

(1) In permanent record books of the Zoology Laboratory.

Brachypterous

males	- pronotum (-)	.975 mm.
	wings (-)	1.94 mm.
females	- pronotum (-)	.99 mm.
	wings (-)	1.932 mm.

The predominance of long winged individuals from southern collecting grounds is marked; among several hundred specimens brought in, only four short winged forms have been recorded. In the Manhattan region, the condition is reversed; Sabrosky's 1932 collection of 594 specimens included only 32 long winged individuals. ⁽¹⁾ In the laboratory the southern and northern forms interbreed freely, their progeny showing as distinct wing dimorphism as did the parents.

The third type, represented by only a few specimens, appears to answer Hancock's description of the austral species, T. lateralis Scudder. Until recently, this name has been applied to the entire greenhouse stock of Tettigidea, but careful examination of the specimens reveals differentiating features. The members of this third group were brought from Houston, Texas, by Nabours, 1935. They are long winged specimens, more slender than T. p. pennata; the anterior pronotal margin in these is broadly rounded rather than angulate, and the faces of the males are more

(1)

In permanent record books of the Zoology Laboratory.

creamy than pure white. Genetic evidence that these represent a distinct race--perhaps a species--will be discussed later.

While there seems to be sufficient reason for thus dividing the specimens into three classifications, previous discussion and uncertainty about these confusing forms makes it seem prudent to present the above ideas only tentatively, to await further verification.

Habitat

Like most Tetriginae, these species are geophilous; but they show only moderate hygrophile tendencies. Their distribution in both campestral and sylvan areas depends upon conditions favoring the growth of algae, lichens, and other simple plants upon which they feed. Unlike Paratettix cucullatus and its allied forms, they do not occur so abundantly along muddy water-margins as they do in damp meadows with soil of sandy loam, or in moist, wooded regions (Morse, 1904). Due, probably, to the extreme summer heat and drowth of the last three years, a marked decline in the Tetrigian population in the vicinity of Manhattan, Kansas, is apparent. Numerous searches of grassy clearings along streams, which in other years have yielded a fair collection of specimens, were entirely fruitless in the

summer of 1937. A few individuals of Acrydium arenosum and Paratettix cucullatus were the only ones seen.

Methods of Rearing

In the greenhouse where the insects are reared, temperature and humidity are regulated to approximate as closely as possible, the year around, optimum conditions of the semi-tropical habitat of the southern forms. The grasshoppers are bred in glass cylinders 8" x 12", covered with screen lids and set in earthenware pots filled with sterilized sand and loam. The food supply, which consists of various filamentous and flocculent algae, is gathered from nearby streams and pools. Tanks in the greenhouse provide the winter supply and afford a supplementary source in summer.

Oviposition in the breeding jars usually occurs from a few hours to several days after copulation, the female selecting a damp, mossy or lichen-covered spot into which 15-25 eggs are deposited, about 5 mm. below the surface. The nymphs, emerging in 17 to 23 days are at first creamy, with red eyes, but become more darkly pigmented within an hour. Due to variability in nymphal hues, it is impossible to discern accurately the ultimate adult coloration until the last ecdysis; neither can one predict the adult wing

phase from general conformation, even during the last nymphal instar. Since critical data cannot, therefore, be taken until development is completed, the high mortality among immature forms greatly retards the collection of sufficient numbers for statistical evaluation.

To prevent promiscuous inbreeding of the stock, the sexes are segregated at about the fourth instar, to be recorded when adult. Except those reserved for mating, the recorded insects are dropped into bottles of 95 per cent alcohol, to be permanently preserved later in sealed vials.

The number of generations produced annually varies with habitat. In nature the sub-tropical forms (Mexico, Texas) probably give 3 or 4 generations a year; those in more rigorous climates (Kansas, Illinois) usually give one or one and one-half generations (Nabours, 1929, 1937). In the greenhouse, the southern lines continue, for at least a year, their rapid multiplication. When they are crossed with the northern forms, the rate falls to two or three generations. The northern variety, provided in captivity with much milder surroundings than they have in nature, may accelerate their breeding rate to produce two, and more rarely, three generations. In all cases, sexual activity reaches a climax in spring and early summer, showing gradual diminution thereafter until about the first of

September. From then until the first of February, the insects appear to undergo a period of torpidity, when they eat noticeably less, and seek hiding places under vegetation or in cracks in the soil. Very few offspring have been produced during this period.

Previous to 1937-1938, the Tettigidea have been kept during cold weather in a room in which the temperature remained about 58°-60°F. This winter (1937-38) however, the room has been kept at 80°-85°F. Observation of the stock under these different conditions has revealed no increase in activity commensurate with the rise in temperature. The tendency of these species toward hibernation in the winter appears to be due to a physiological state not immediately altered by 20 degrees change of temperature. Under the conditions noted, no difference was discernible between the activity of northern and southern forms.

EXPERIMENTAL DATA

Approximately one-half of the data used in this study were taken from Nabours' permanent record books, covering the period from June, 1932, when short winged individuals from the vicinity of Manhattan were added to the southern long winged stock, to January, 1937. The rest of the data have been collected mainly during the year 1937. A total of 222 productive matings, with 4313 adult offspring recorded, have been analyzed for the possibility of a wing length gene or genes, and for color patterns.

In Table 1 is given the complete pedigree of all productive matings during the period described, with reference to the incidence of long wings and pronota (lw) and short wings and pronota (sw). Assuming the factor for short wings and pronota (S) to be a simple dominant having a recessive allelomorph (s) for long wings-pronota, three genotypes should occur: S/S, S/s, and s/s. Since dominance is complete, the first two types are indistinguishable. All of the matings fall into six classes or categories:

A. S/? x S/?, both sw. This includes individuals from the field, and those from crosses involving no recessive to establish their heterozygosity. If, however, the mating

Table I.

Matings of *Tettigidea parvipennis* and *T. p. pennata*, showing incidence of long and short pronota and wings*

A. S/? x S/?										D. S/? x s/s										E. S/s x s/s										F. s/s x s/s									
Matings		Source		s/s		S/?				Matings		Source		s/s		S/?				Matings		Source		s/s		S/s				Matings		Source		s/s					
Book: Page	Book: Page									Book: Page	Book: Page									Book: Page	Book: Page									Book: Page	Book: Page								
63 220	63 J.C.	F ₂ 's			8	12				63 235	63 220				1	7				66 6	63 236			2	0	2	1			177	135		1	0	0	1			
233	220				0	1				236	221	R				8	2			65 66	6			1	0	1	1			178	138		2	0					
234	220				1	0					220									179	6									179	140		4	6	5	1			
66 7	N.B.			1	0	0	1			238	231	R				0	2			70 63	J.C.			4	5	9	3				128								
66 66	J.C.			0	1	5	4				220										236									132	R	0	1						
256 66	158					1	6			240	220									71	237	T	R	0	4	0	1			190	129								
70 150	53F ₂			2	3	2	8				231									77	235			2	1	5	1			191	132		5	1	0	3			
145 70	53F ₂			5	4	12	7			66 52	J.C.			6	5	11	10				236									192	136								
73 98	S					53	24			54	J.C.					5	2				237	T	R	31	17	27	20			193	140		1	1					
	stray									73	J.C.					15	17													194	129		8	4	3	8			
119 73	22			1	0	3	6			76 66	7	R				2	0				240									195	129								
138 10	5									79	7	R			0	1	1	0			64									196	128		5	3	8	7			
										97	T	R					1	3			77	R		6	6	9	8			197	129		2	0	0	4			
											J.C.										53									238	129		0	1		3			
										147	67	R			2	0	0	1			52			2	1	0	1			271	174		0	2					
										170	70	R					0	2			67	R		2	3	2	0			272	H		0	4					
										270	66						1	0			73			2	3	4	3			275	240								
										285	161	R			3	2	2	3			64									195	198		20	27	34	29			
											163										70			10	2	9	3			276	197		28	19	26	23			
										294	255	R			2	2	5	4			99									198	191								
											256										67									277	143		18	15	25	14			
										297	256	R			9	4	3	0			67	R		0	1					286	175		22	21	11	20			
											256										147			0	2					287	142								
										70 3	66										76			0	2					288	176		22	33	42	31			
											211										76			1	0	2	2			289	191		13	16	11	20			
										22	255										71									290	156								
										23	255										51	R		2	2	1	2			291	179								
										24	269										73									292	158		0	5	7	5			
										25	255	R									67									293	143		0	5					
										48	256										70	R		1	0	0	1			294	179								
											271	R			1	5	5	3			70									295	132								
											296										52									296	153		8	14	4	8			
										51	255										52	R		1	0	0	1			297	143								
										54	271	R									52									298	191								
											255										150									299	177		8	12	8	10			
										55	297	R			1	0	1	1			99			2	3	3	4			300	173		8	12	8	10			
											255										73			4	4	3	3			301	196		14	5	8	12			
											171										154	R		4	3					302	179								
										142	70										152									303	158		1	1	1				

thus recorded ($\underline{S}/?$ x $\underline{S}/?$) produced any $\underline{s}/\underline{s}$ offspring, it thereby proved its composition to be actually $\underline{S}/\underline{s}$ x $\underline{S}/\underline{s}$, and the progeny were counted with those of class "C" (Table 2, b).

B. $\underline{S}/?$ x $\underline{S}/\underline{s}$, both sw, one a known heterozygote. If, as in "A", any $\underline{s}/\underline{s}$ progeny appeared, the heterozygosity of both parents was established, and the offspring were totaled with "C" (Table 2, b).

C. $\underline{S}/\underline{s}$ x $\underline{S}/\underline{s}$, both sw, known heterozygotes.

D. $\underline{S}/?$ x $\underline{s}/\underline{s}$, one sw, genotype uncertain from its parentage, and one recessive. If such a cross gave any $\underline{s}/\underline{s}$ offspring, the sw parent was thereby proved to be $\underline{S}/\underline{s}$, and the offspring were totaled with those in "E" (Table 2, a).

E. $\underline{S}/\underline{s}$ x $\underline{s}/\underline{s}$, one sw heterozygote, one recessive.

F. $\underline{s}/\underline{s}$ x $\underline{s}/\underline{s}$, both recessives (lw).

Under these headings, data are listed in order of their occurrence in the permanent record books, indicated in the columns headed "Mating". Under "Source" are listed the book and page number in which the parents of the mated individuals are recorded (source of male given first).

Letters indicate the source of specimens from the field:

"S" Santiago; "T" Tampico; "VC" Vera Cruz, in Mexico; "H" Houston; "SA" San Antonio; "G" Georgetown; "NB" New

Braunfels, in Texas; and "JC" Jones' Cabin, one mile east of Manhattan, Kansas, the only source of the northern stock. Long winged offspring are listed in the s/s column, and short winged at the right. An "R" beside the source pages indicates that the mating is the reciprocal of that given at the head of the class. It is thus possible to trace the pedigree of any mating back to its sources in the field. For example, C66-155 denotes a mating under class C, book 66, page 155. All "C" matings are S/s x S/s. Both parents (see "Source" column) are from book 66, page 99. Since S/s individuals are products of S/s x s/s, the source of this mating will be found under class D or E. In this case it is at E66-99. "R" indicates that the male was s/s; and he was brought from "T" (Tampico). The female S/s, from 63-240, had her source in D or E. Located at D63-240, this mating may then be traced back to F63-163, which was the line of s/s stock brought from "SA" (San Antonio), 1929; and to A63-220, brought from "JC" (Jones' Cabin), 1932.

Matings of Specimens From the Field

Certain of the following earlier matings were marked S/? in the table, but their progeny established them as S/s:

S/? x S/?, both northern (A66-66) gave 9 S/?:1 s/s.

Parents must therefore have been S/s x S/s.

Two crosses S/? (north) x s/s (north); D66-52 gave 21 S/s:11 s/s, and the sw parent was thus shown to be S/s. D66-54 gave S/s 7, leaving uncertainty as to heterozygosity of S/? parent.

Two crosses S/? (north) x s/s (south); D66-76 and 97 produced S/s 2 and S/s 4, respectively.

S/? x S/?, both southern (A66-7) gave 1 S/?:1 s/s, showing that both parents were S/s. The S/? offspring was non-productive; the s/s functioned in D66-76 above.

S/? (south) x two sw females, one S/? (A73-98), the other S/s (B73-22) produced 92 S/? offspring. One inbred generation from A73-98 has shown only sw.

Nine F_2 progeny of the original sw pair (A63-220) were used in matings (A63-233, 234; D63-235, 236, 238, 240; and D66-79). The inbred mating at A63-234 is noteworthy; because the one S/?, when mated to an s/s (66-73) gave 32 progeny, all sw. The S/? was apparently, therefore, homozygous (S/S).

Both northern and southern lw form behaved as recessives (E66-6 and 99; F66-5, 8, 50; D66-52 and 54; and others).

Numbers of Offspring

Table 2 is a summary of Table 1, showing the total numbers of lw and sw males and females from each kind of cross. The totals for S/s x s/s include all class E matings; and all those under D which demonstrated the heterozygosity of the sw parent by producing some s/s offspring, except the following, in which the virginity of the female at the time of mating was questionable: D66-52, 79; D70-142, 143, 144, 155, 156; D73-93, 133. Totals of S/s x S/s include all class C matings; also the following ones from A and B which produced some s/s, and the female was known to have been virgin when recorded; A73-138, and B66-296. Totals for s/s x s/s include only category F. The other three types include those matings of A, B, and D in which the heterozygosity of S/? remained a question. S/? x S/s includes B matings (except 66-296, above), and those matings from A in which the females, while probably non-virgin, must have been S/s; for s/s offspring were produced.

Table 2, a, shows the results of 121 matings, S/s x s/s, 2454 offspring. Theoretical ratio 1:1 or 1227:1227. Deviation 41, or 2.45 times the probable error.

Table 2

Summary of Table 1, Showing Total Offspring of Six Types of
Crosses of Tettigidea parvipennis and T. p. pennata.

Mating	lw		sw		total		theoreti- cal ratio		devia- tion : dev./P.E.	
	males	females	males	females	lw	sw	lw	sw		
a. S/s x s/s	605	581	653	615	1186	1268	1227	1227	41	2.45
b. S/s x S/s	121	113	248	238	234	486	180	540	54	7.27
c. s/s x s/s	337	332			669		669	0	0	
d. S/? x S/?			66	49		115				
e. S/? x S/s	14	9	53	38	23	91				
f. S/? x s/s	25	23	92	101	48	193				
	1102	1058	1112	1041	2160	2153				

Table 2, b, shows S/s x S/s, 31 matings, 720 offspring. Theoretical ratio 3:1, or 540:180; actual ratio 486:234. Deviation 54, or 7.27 times the probable error. Applying a theoretical ratio of 2:1 (480:240), the deviation is only 6, or .702 P.E.

s/s x s/s, 31 matings, 668 offspring, all long winged (s/s).

Relation to Other Characters

Bellamy (1917) has described six color patterns in T. parvipennis pennata, five of which constitute an allelomorphic or an extremely closely linked series, the sixth occurring in connection with or in addition to one or more of them. The series includes C, white dorsal stripe; D, bilineate pattern extending the full length of the lateral carinae; E, ill-defined mottling on a pallid background; F, distinct white spot on posterior femora; M, dark brownish gray to black. The sixth pattern, H, all-over brown, probably segregates independently of the other five, as is shown in Table 3.

Table 3

Segregation of Color Gene H (Brown) With Patterns
of Allelomorphic Series.

(Including Data of Bellamy, 1917)

Factors	Specimens	Segregation	% Segregation
DH	351	163	46.44
EH	501	268	53.49
FH	439	224	51.02
CH	442	191	43.21
Total	1733	846	Ave. 48.83

Of these patterns, only C, F, and H are definitely recorded in the present stock. Tests for possible linkage of the short wing gene S with the three patterns show segregation in an average of 50.12 per cent of 832 cases, with extremes of 43.81 per cent and 54.81 per cent.

In addition to these patterns, another has been noted --a grayish cast over the entire body surface, which is almost invariably associated with lw, and causes s/s specimens to look grayer, even in immature stages, than those carrying S. It has been possible, with practice, to pre-

dict adult wing phases of more than 200 nymphs with 90 per cent accuracy. This gray "factor" b behaves as a recessive closely linked with s (Table 4).

Table 4
Segregation Ratios of the Wing and Pronotum Gene
(S) With Color Patterns, and of a Recessive
Gene (b) With (s).

Factors	Males			Females		
	Specimens	Segre- gating	% Segre- gating	Specimens	Segre- gating	% Segre- gating
CS	121	53	43.81	135	74	54.81
HS	162	82	50.61	121	62	51.24
FS	9	4		5	4	
Totals	292	139	Av. 47.21	261	140	Av. 53.025
bs	619	4	.646	628	7	.111

Six matings of southern s/s specimens from the vicinity of Houston, Texas, non-productive when mated with greenhouse stock, have been shown to differ morphologically from the usual lw forms. They conform closely, as stated before, to Hancock's description of T. lateralis, and are fertile when bred together (F73-21, 121, and 141). Only one male of this type survives in the present stock, mated

to a BS/bs C/F +/H. Two offspring have hatched, but while as yet too small to record, they are females, apparently bearing the maternal coloration, and are probably parthenogenetic.

Three cases of parthenogenesis are on record, all s/s, but none has produced a second generation.

DISCUSSION

The three categories of known genotype matings give evidence of a simple Mendelian unit determining wing and pronotum length. Recessives breed true; heterozygotes x recessives give a ratio (1268:1186) well within probability for the expected 1:1 distribution. In heterozygote crosses, however, the 468:222 approaches, not a 3:1, but a 2:1 ratio, deviation from the latter being only 6, or .702 P.E. This at once suggests the possibility of a lethal factor l linked with S. Were this the case, a heterozygous mating Sl/s x Sl/s would give 1 Sl/Sl (lethal), 2 Sl/s (not lethal), and 1 s/s, with a 2:1 ratio resulting.

All the present sw stock except those recently brought from the South (B73-22) are descendants of the northern pair A63-220. Assuming that a lethal mutation occurred in the sw population of the Manhattan region, it appears probable, from the composition of the offspring, that these

progenitors were Sl/s x S/Sl (or reciprocal). Four types of non-crossover offspring would be produced: Sl/S, S/s, Sl/s, and Sl/Sl (lethal). F₂'s could then be Sl/Sl (lethal), Sl/S, Sl/s, S/S, S/s and s/s.

The seven matings involving the F₂'s suggest the following composition:

(1) A63-233 (inbred): 1 sw, none bred forward; could have been any S combination.

(2) A63-234 (inbred): 1 sw. This offspring x s/s (D66-73) gave 32 sw progeny; it was probably S/S or Sl/S. Of the inbred matings from these 32 sw, 2 (C66-144, 156) gave 2:1 ratios, while 2 others (C66-158, 161) gave approximately 3:1 ratios. In crosses of sw from D66-73 x s/s, the rather scant critical data show that subsequent sw x sw matings probably carried the lethal. These all seem to indicate that the one offspring of A63-234 was Sl/S.

(3) D63-235 (S/? x s/s): 8 sw; no critical matings to test for presence of l; probably S/S or S/Sl.

(4) D63-236 (S/? x s/s): 10 sw. Heterozygotes inbred (C65-72) gave a ratio of 34 sw:7 lw. Crossed with other heterozygotes, they gave (C66-53) 21 sw:11 lw, and (C66-80) 12 sw:9 lw. These indicate also the possibility of an Sl/S. The mating giving the 34:7 ratio was not carried

forward.

(5) D63-238 (S/? x s/s): 2 sw; insufficient data for analysis.

(6) D63-240 (S/? x s/s): 4 sw. Only one critical mating (C66-155)--4 offspring, 2 sw, 2 lw; could have been any S type.

(7) D66-79 (S/? x s/s): 1 sw:1 lw. Sw must have been Sl/s or S/s, giving evidence of heterozygosity of stock.

Other sw matings from nature were not bred forward to give sufficient data on l.

Whether it be due to greater fertility or vigor, or merely to chance selection, heterozygous matings carried forward have practically all been of the type thought to carry the lethal.

Southern sw forms show no evidence of a lethal. Ninety-two offspring, all sw, from one male are sufficient evidence of his homozygosity, and one inbred generation, all sw, seems to establish it further.

Linkage tests indicate three pairs of autosomes as bearers of the genes now identified: C, F, E, M, and D on one pair; H on another; the wing determiners S and s with the linked genes b and l on the third.

CONCLUSION

This study of 4313 specimens gives significant evidence that a single hereditary unit, modified by a linked lethal, but apparently independent of environment, is responsible for wing and pronotum dimorphism in T. parvipennis and T. p. pennata. Nine genes have been identified, which segregate into three independent sets, and probably represent three pairs of autosomes.

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